

Introduction

In the last decade, studies of parental care have rapidly proliferated. This increased interest in parental care has been stimulated by advances in three fields. First, the revolution in molecular biology has generated techniques that are increasingly used by behavioural scientists. Such techniques include DNA fingerprinting, which allows researchers to identify the genetic relatedness between putative parents and offspring, and molecular sex markers that allow researchers to determine the sex of offspring at an early stage before external differences have developed. In addition, gene sequencing, which is now fast and relatively inexpensive, has generated vast quantities of data, which are increasingly used to reveal evolutionary relationships that complement older morphology-based phylogenies. This has led to the second advance: several novel statistical techniques, which include parsimony and maximum-likelihood methods for phylogenetic reconstructions, have been developed to investigate past evolutionary events. These techniques provide new opportunities to examine the origins of parental care behaviour, the direction of parental care evolution and life history traits that may have influenced parental care evolution. Third, mathematical modelling of parental care has matured and now encompasses a range of game-theoretical models, some of which take account of state dependence and stochasticity. There has also been an effort to consider the feedback loops between parenting decisions and mating decisions. Some of these models were motivated by the growing consensus that parental care is one of the main battlefields for conflict between the sexes. New mathematical models have been essential in understanding aspects of these conflicts.

Motivated by the growing interest in parental care and by the fact that theoretical and empirical investigations were being conducted largely independently, we decided to organize a workshop. We aimed to create an environment in which new results and ideas in parental care research could be reviewed and discussed, where theoreticians and empiricists could interact and where the major unresolved issues and future directions could be outlined. The workshop took place in the village of Bernried in Bavaria (southern Germany) from 4–7 August 2000, and was attended by 44 participants from around the world. The papers in this theme issue reflect the key contributions presented at the workshop. We hope that this issue will serve as a roadmap for some of the exciting developments in parental care research.

This issue (like this Introduction) is divided into two major sections. The papers in the first section review the current thinking about the origins of parental care and the courses of evolution from one form of care to another.

The papers in the second section explore various factors that are thought to influence parental behaviour; § 2a covers the effect of sexual conflict on parental care, § 2b is concerned with the effect of paternity on parental care, and § 2c reviews the evidence that parents bias the sex ratio of their brood or the care they provide to particular offspring.

1. THE ORIGINS AND PATHWAYS OF PARENTAL CARE

There have been many theoretical explanations for why parental care originally evolved in some animal groups and there has been much debate about how one form of care might lead to another. The papers in the first section of the issue reflect this interest and represent one of the central themes of the workshop, *the origins and evolution of parental care behaviour*. In the first contribution, Burley & Johnson (2002) use life history and behavioural traits in extant species to develop a logical stepping-stone verbal model for the evolution of biparental care in modern day birds. They argue that biparental care and monogamy in birds evolved from a promiscuous mating system with no parental care via a stage of female-only care. Following the evolution of female-only care, females would have been a more limited resource for male reproductive success, allowing females to demand parental investment from males in return for mating access. Using a formal parsimony approach, Tullberg *et al.* (2002) also examined the origins of parental care in birds and reached similar conclusions. Their historical analysis indicates where on the phylogenetic tree various care forms evolved. These authors show that female-only care appears to have evolved in an ancestor to birds and that biparental care evolved from female-only care in the ancestors to modern day birds. When combined, these papers constrain the potential evolutionary scenarios and provide a starting point for more detailed analyses of avian mating systems.

The evolution of parental care should be driven by the relative costs and benefits of providing care (Maynard Smith 1977; Clutton-Brock 1991). To investigate this, researchers have used the variation within and among animal groups in the extent to which males and females care for offspring. Consistent differences in life histories and ecologies among closely related species that differ in parental care can be used as evidence for the trade-offs associated with parental care. An exciting example of such studies is represented in this issue by Goodwin *et al.* (2002). They explore the ecological correlates of the evolution of live-bearing in fish by matching pairs of taxa so that each group consists of a closely related egg-laying and live-bearing clade. Their results suggest interesting life history trade-offs that might explain the evolution of live bearing. For example, they show that live bearers tend to be larger than their egg-laying relatives and that

they produce larger offspring. Reynolds *et al.* (2002) provide a comprehensive review of parental care modes across an extremely broad range of taxa (from primates to sea spiders). Their analyses indicate that there have been *many* transitions in care forms. They provide evidence that various ecological conditions set the stage for the evolution of uniparental care from biparental care and argue that sexual selection may maintain female care. In contrast to the previous two contributions that compare mainly closely related species, the last paper in this section by Owens (2002) suggests that sometimes it is appropriate to compare more ancient lineages (i.e. families). Owens uses a family-level paired comparison to examine the occurrence of male-only care in birds. *Within* birds, male-only care is rare and has thus attracted a great deal of attention. Despite the great interest, no consistent ecological difference between species showing male-only care and closely related species showing other patterns of care has been found. Owens argues that in birds, male parental care may be highly conserved phylogenetically and thus it makes sense to compare ancient lineages containing male-only versus female-only care. He finds a striking difference in breeding or nesting densities, suggesting that sex differences in re-mating opportunities may be linked to the evolution of male versus female care in birds.

The use of (phylogenetically controlled) comparative approaches to understand parental care evolution is recent and there was both widespread support, and criticism, of the method at the workshop. Critics of the approach argued that the usefulness of these methods is often hampered by crucial missing phylogenetic information, which can lead to unknown biases or faulty conclusions. Across species, the form of parental care differs and it remains unclear how to compare across taxa in a meaningful way. Proponents of the technique argued that evolutionary history simply cannot be addressed with experiments; it is impossible to answer questions about the origins and pathways of care in other ways. Broad patterns across species can generate extremely persuasive arguments to support evolutionary hypotheses. Another criticism levelled at the comparative approach was that causation is impossible to detect. However, unless the two traits in question are tightly correlated or changing simultaneously, by examining a phylogeny it is possible to observe which trait generally precedes the other (Sillén-Tullberg 1988, 1993). Critics of the comparative approach argued that life history trade-offs occur at the level of the individual and cross-species comparisons can therefore reveal little of these trade-offs. However, if the responses to selection are sufficiently strong and general, it is possible to see them in comparisons among related taxa. We feel that this issue's contributions highlight the merits of the comparative approach.

2. FACTORS AFFECTING PARENTAL CARE

(a) *Sexual conflict, mate choice and parental care*

Traditionally, sexual selection models have emphasized that relative parental investment, potential reproductive rates and operational sex ratios and variation in mate quality influence the intensity of competition and the degree

of mate selectivity (choosiness) (Trivers 1972; Clutton-Brock & Parker 1992; Arnold & Duvall 1994; Johnstone *et al.* 1996). Recent work has highlighted the strong reciprocal interactions between parental care and sexual selection. Relative parental investment may determine the degree of sexual selection, but the degree of sexual selection will probably have a feedback effect on parental care decisions (Reynolds 1996; Székely *et al.* 2000). For instance, the role of variation in investment over time within an individual (and the resulting sexual conflict) on mating and parenting strategies has only begun to be examined. The second theme of the workshop: '*sexual selection and parental care*' concerned this growing area of research.

The first paper by Parker *et al.* (2002) examines the effects of conflicts between family members on parental effort. Their model shows that all conflicts (sexual, parent-offspring and sibling) must be considered simultaneously to resolve what share of parental investment each chick will receive. They argue that uniparental care can actually be more effective than biparental care when the negative effects of sexual conflict are taken into account. In a recent experiment with zebra finches, Nick Royle and his co-workers supported this prediction (Royle *et al.* 2000).

Females may choose a mate based on his ability or willingness to provide care. Sometimes preferred mates invest most, sometimes least. Bussière (2002) provides a novel theoretical explanation for the observed variation. In some species (e.g. courtship feeding insects) females receive direct benefits (nuptial gifts) and sperm during mating. Bussière shows that there may be selection on preferred males to provide smaller gifts compared with less-preferred rivals, if pre-mating female choice biases the perception of mate availability of preferred males relative to their rivals. Under such circumstances, preferred males should gain by conserving resources for future matings. However, since preferred males are often in better condition, a positive correlation between male quality and gift quality might be observed, even if the true optimum for preferred males would be smaller than that for less-preferred males. This idea requires experimental testing.

Kokko & Johnstone (2002) explore the rarity of mutual mate choice in animals. They show that the strong tendency of sexual strategies to diverge hinders the evolution of mutual choice. Mutual choice will be favoured if synergistic benefits of biparental care greatly improve offspring survival and if the parental investments of both sexes are high and not too different. Webb *et al.* (2002) use a state-dependent dynamic model to investigate how changes in the levels of energetic reserves during the season affect parental care decisions. These papers are among the first to examine how asymmetry of parental investment and variation in individual quality can interact with potential variation in parental care (quality and quantity), leading to a better understanding of sexual selection. Testing these ideas will be feasible in only a few taxa, where experimental manipulation is not too difficult. Theoretical modelling is essential to consider the many factors involved in care decisions and to tease apart the interactions between these factors (Balshine-Earn & Earn 1997; Webb *et al.* 1999).

(b) Certainty of paternity and parental care

It makes sense that parents will invest energy and time in raising young only if these young are their own. But how certain can males be that the young in the nest are their own? What cues do they use to assess paternity? How should they respond? Sheldon (2002) reviews the current models of how certainty of paternity influences paternal investment. Some experimental evidence supports the existence of facultative responses to certainty of paternity (in agreement with the models), while other studies do not. Sheldon argues that testing these models directly is difficult, if not impossible, because of two fundamental problems. First, we are not measuring (and perhaps cannot measure) the most relevant variables. We can quantify the amount of care delivered by a parent (its duration, its frequency), but this is not the same as measuring parental investment. We can quantify paternity in a brood, but this is not the same as measuring 'certainty of paternity'. The models can only be tested adequately by experimentally manipulating certainty of paternity. However, if certainty of paternity cannot be measured, it is impossible to distinguish between an experiment that fails to manipulate certainty of paternity versus the absence of a response to the manipulation (Wright 1998). Second, Sheldon points out that the models do not capture the complexity of real systems. For example, experimental manipulations where males or females are kept away from their mate may have unintended consequences. Female removal could elevate male testosterone levels, which may lead to reduced parental care. Nevertheless, Sheldon reviews his own studies on collared flycatchers to provide a qualitative test of the models.

The models predicting a relationship between certainty of paternity and parental care suffer from another serious problem: they are not self-consistent. If a male has lost paternity then other males must have gained paternity. Houston & McNamara (2002) point out that the fact that the total reproductive success of all males must equal the total success of all females has important implications for the expected relative effort of males and females. Houston and McNamara provide an incentive to develop further self-consistent models that include the possibility that males differ in their ability to provide care or to obtain additional matings. This would make models more realistic, because males are known to differ in characteristics that influence care or paternity (e.g. condition or age). Houston and McNamara point out that there are other important feedback loops that need to be considered in more realistic models. For example, in biparental species, the amount of care a male provides should depend on the amount of care provided by his mate and vice versa. The optimal investment is also related to re-mating opportunities and other aspects of the ecology and the life history of an animal.

(c) Biases in sex allocation and parental favouritism

The advent of molecular sex determination has stimulated a surge of studies investigating whether, and how, parents might adaptively bias the sex ratio of their brood. Contributions by Hasselquist & Kempenaers (2002) and by Komdeur & Pen (2002) review the current renaissance of sex allocation studies. Factors thought to correlate with

sex ratio adjustment in birds include food abundance, maternal condition and mate quality. Hasselquist and Kempenaers explicitly discuss how females might respond in terms of sex allocation to expected differences in paternal care. Both papers conclude that the hypothesis that females can bias the primary sex ratio in relation to parental quality and environment remains generally unconfirmed. The key obstacles in assessing the hypothesis are the probable publication bias against non-significant results and the lack of information about the mechanism for primary sex ratio bias. A novel suggestion was made at the workshop: to set up a website that functions as a controlled repository for non-significant results. Hasselquist and Kempenaers call for more large-scale correlational studies that ensure high statistical power, as well as studies that experimentally manipulate primary sex ratio and investigate fitness effects. Komdeur and Pen strongly advocate that fieldwork should turn away from correlational studies to an experimental approach.

Sometimes, after the young emerge, parents play favourites. What selects for such parental favouritism? Why would two parents care differentially for different individual offspring or different kinds of offspring? Lessells (2002) mathematically explores four traditional explanations for parental favouritism. Her analysis suggests that evolutionary conflict (either between parents and offspring or between the two parents) is probably the most important selective force favouring the evolution of parental favouritism.

In conclusion, the workshop provided an unparalleled opportunity to discuss the past, present and future of parental care research. The papers contained in this issue summarize some of the highlights of the meeting, including reviews of new theoretical ideas and empirical findings, and discussions of current controversies and unsolved problems. We hope that the research described in this issue stimulates many further developments in our understanding of parental care.

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